The Role of Within-Host Competition for Coexistence in Multiparasitoid-Host Systems

van Velzen, Ellen; Perez Vila, Saleta; Etienne, Rampal S.

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The Role of Within-Host Competition for Coexistence in Multiparasitoid-Host Systems

Ellen van Velzen,* Saleta Pérez-Vila, and Rampal S. Etienne

Groningen Institute for Evolutionary Life Sciences, University of Groningen, PO Box 11103, 9700 CC Groningen, The Netherlands

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abstract: Multiparasitism (females of multiple species parasitizing the same host) is a ubiquitous phenomenon in parasitoids, yet the role of within-host competition has been mostly ignored in multiparasitoid-host models. Here we study the effect of varying the degree of competition at different life stages: competition over oviposition sites (between-adult competition) and larval competition over resources within the host (within-host competition). We adapt a Nicholson-Bailey model to allow for varying levels of between-adult competition (varying the overlap in species distributions) and within-host competition (varying the number of offspring that can successfully emerge from a host). Surprisingly, while stronger between-adult competition reduces coexistence, stronger within-host competition promotes it. Asymmetric between-adult competition (a fecundity difference between the two species) reduces coexistence when compared to symmetric competition; this can be counteracted by asymmetric within-host competition (within-host competitive advantage of the lower-fecundity species), but only when within-host competition is strong and the correlation between the parasitoids' distributions is intermediate. We discuss our results in the context of the interaction between two parasitoid species, *Nasonia vitripennis* and *Nasonia girault*i, which have strongly correlated distributions and high levels of multiparasitism in the field. We conclude that either low or asymmetric within-host competition is unlikely to explain their coexistence.

Keywords: host-parasitoid, multiparasitism, coexistence, within-host competition, *Nasonia vitripennis*, *Nasonia girault*i.

Introduction

To maximize their fitness, female parasitoids must choose their hosts in such a way that they maximize their offspring's success (optimal oviposition theory; Jaenike 1978). The expected optimal oviposition strategy is to exploit a host by herself so that her offspring will not have to share resources with competitors (Godfray 1994; van Baaren et al. 1994; Crespo and Castelo 2009). However, superparasitism (parasitizing a host already used by a conspecific female) can be an adaptive strategy (Charnov and Skinner 1984; van Alphen and Visser 1990; van Alphen et al. 1992), for example, when hosts are scarce and searching for unparasitized hosts would be inefficient. Superparasitism is indeed frequently found in nature (van Alphen and Visser 1990; Godfray 1994; Dorn and Beckage 2007). While superparasitism does not necessarily lead to intraspecific host sharing (offspring of multiple females successfully emerging from the same host), this is common in gregarious species (Harvey et al. 2013).

In contrast, interspecific host sharing is very rare (reviewed in Harvey et al. 2013). Multiparasitism (parasitizing a host already used by a heterospecific female) is adaptive under only two scenarios: if the offspring of one parasitoid do not consume the entire host or do not require the entire host to develop (Miller 1982; Magdaraog et al. 2012) and if the multiparasitizing female has a competitive advantage over the first. The latter is the rule: one species wins within-host competition, and a range of mechanisms for eliminating competitors have been found in species faced with interspecific within-host competition (e.g., see Fisher 1963; Hagvar 1988; Chau and Maeto 2008; Harvey et al. 2013). Thus, while multiparasitism is common, it rarely leads to interspecific host sharing. A detailed explanation for this is still lacking.

Perhaps because interspecific host sharing is so rare, it has received relatively little attention in theoretical studies. Most multiparasitoid-host models assume that either one species always arrives first and the second species does not multiparasitize or one species is always competitively superior (May and Hassell 1981; Kakehashi et al. 1984; Klopfer and Ives 1997; Porter and Hawkins 2003; Lane et al. 2006; Kon and Schreiber 2009). In some other models, the outcome of multiparasitism is decided by who arrives first (Hogarth and Diamond 1984; Hackett-Jones et al. 2009). Most of these models consider solitary parasitoids, in which complete competitive superiority is a reasonable assumption, but even the models that do include gregarious parasitoids (Klopfer and Ives 1997; Lane et al. 2006; Kon and Schreiber 2009) do not include the possibility of host sharing. Only one study explicitly looks at the effect of within-host competition on coexistence in solitary parasitoids (Hogarth and Diamond 1984)

* Corresponding author; e-mail: ellen.v.velzen.2@gmail.com.

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and finds that the competitive superiority of either species has negligible effect on the likelihood of coexistence. However, this model may be too simplistic, incorporating the probability of winning within-host competition as a constant that does not depend on the abundances of the two parasitoid species. This may be appropriate when considering solitary parasitoids, but in gregarious parasitoids for which superparasitism and host sharing are common, the abundances of the two species and therefore their encounter rates with the hosts should be incorporated into how within-host competition plays out.

Another strong limitation of current models is that the number of parasitoid offspring emerging from a host is always the same, regardless of how many times it is parasitized; the only distinction these models make is between parasitized and unparasitized hosts, ignoring the exact number of encounters. Again, this is appropriate for solitary parasitoids where only a single offspring can emerge, but in gregarious parasitoids, superparasitism may increase the brood size as more eggs are laid (e.g., see Molbo and Parker 1996; Gu et al. 2003). Therefore, both the total number of emerging offspring and the relative contribution of each species to this number critically depend on the number of times each individual host is parasitized by either species; however, this is missing from all current multiparasitoid-host models. Hence, a proper model for multiparasitism and its effects on coexistence is still lacking. Our aim in this study is twofold: first, to develop a model for gregarious parasitoids to study the effect of multiparasitism more closely, and second, to apply this new model to understand the coexistence of two closely related parasitoid species, *Nasonia vitripennis* and *Nasonia girault*i, which we will introduce in the next section. We develop the model with this system in mind, but the results are applicable to multiparasitoid-host systems in general.

The Nasonia *System*

Nasonia (Hymenoptera: Pteromalidae) is a genus of gregarious parasitoid wasp species, laying several eggs in one host. They are the main parasitoids of the pupae of *Protocalliphora* spp. (Diptera: Calliphoridae), blowflies whose larvae parasitize young birds. In the field, *Nasonia* are collected from bird nests. Individuals mate at emergence on the natal patch, including sib mating, and females then disperse to find suitable hosts (Whiting 1967). Four species have been described in this genus, of which three have a limited geographical distribution: *Nasonia longicornis* in western North America and *N. girault*i and *Nasonia oneida* occurring sympatrically in eastern North America. They all co-occur with the fourth species, *N. vitripennis*, which has a worldwide distribution (Darling and Werren 1990).

We illustrate our model with *N. vitripennis* and *N. girault*i because their coexistence is puzzling. *Nasonia girault*i has a lower attack efficiency and a longer handling time per host (S. Pérez-Vila, personal observation) and lays fewer eggs per host (Grillenberger et al. 2009; Daoust et al. 2012). Yet despite its obvious inferiority, it has not been competitively excluded, although its abundance in the field is much lower than that of *N. vitripennis* (Grillenberger et al. 2009; Daoust et al. 2012). Coexistence of competing parasitoids where one parasitoid is an objectively inferior competitor is possible if the inferior competitor is able to avoid competition with the superior one. This can occur through spatial or temporal resource partitioning, for example, if interspecific aggregation is weak compared to intraspecific aggregation (Ives 1988*a*, 1988*b*; Hartley and Shorrocks 2002) or if the inferior competitor has access to refuges that are not parasitized by the superior competitor (e.g., van Nouhuys and Punju 2010). This appears to be an unlikely explanation for the interaction between *N. vitripennis* and *N. girault*i, because interspecific aggregation is actually very strong: *N. girault*i is always found together in the same nest with *N. vitripennis*, and both multiparasitism and host sharing between the two species are common (Grillenberger et al. 2009). It is also clear that within-host competition affects fitness: offspring body size is determined by nutrient availability during development, with overcrowding causing smaller offspring (Rivero and West 2005; Sykes et al. 2007), and body size is correlated with longevity as well as lifetime fecundity in *N. vitripennis* (Flanagan et al. 1998; Rivero and West 2002; Sykes et al. 2007). Although these fitness effects have been studied only in *N. vitripennis*, they can be expected to be the same for other *Nasonia* species. In addition, multiparasitism comes at an additional cost to offspring compared with superparasitism: the offspring of heterospecific competitors are not suitable as mates, leading to wasted time and energy by courting and mating with the wrong species, which cannot lead to viable offspring due to incompatibility caused by *Wolbachia* bacteria (Breeuwer and Werren 1990).

Because of the higher cost of multiparasitism compared with superparasitism, we should expect *Nasonia* species to avoid multiparasitism more strongly than superparasitism and to prefer empty hosts over either superparasitism or multiparasitizing. These patterns hold for multiparasitism between *N. vitripennis* and *N. longicornis*, which is rare in the field, and experimental evidence shows that both species avoid multiparasitism more strongly than superparasitism (Ivens et al. 2009). In contrast, multiparasitism rates between *N. vitripennis* and *N. girault*i in the field are high (Grillenberger et al. 2009). Even more surprisingly, a host choice experiment suggests that *N. girault*i prefers multiparasitizing over parasitizing an empty host (S. Pérez-Vila, L. W. Beukeboom, R. S. Etienne, and B. W. Wertheim, unpublished manuscript), which seems to directly contradict optimal oviposition theory. This suggests that multiparasitizing may confer an advantage to *N. girault*i, and this could poten-

tially explain its persistence in competition with *N. vitripennis*. While little information is available about the relative competitive abilities of the two species within the host and there is no indication that either species engages in within-host combat or has morphological adaptations for winning within-host competition, the high incidence of multiparasitism and host sharing alone makes the effect of within-host competition on coexistence worth investigating.

Overview of Modeling Approach

In this article, we extend a standard Nicholson-Bailey model for host-parasitoid interactions in discrete time (Nicholson and Bailey 1935) to two parasitoid species with correlated distributions and combine this with individual-based simulations to study the effects of between-adult and within-host competition more closely. Specifically, we study the effect of three factors: (1) varying the level of overlap between the distributions of the two species under either symmetric or asymmetric competition, the latter being implemented through a difference in fecundity between the two species; (2) varying the maximum number of offspring that can emerge from the host (if this is high, multiple females may use the same host without severe competition over resources); and (3) introducing asymmetric interspecific competition within the hosts. For 1, we used both the analytical framework and individual simulations; for 2 and 3, the equations do not give a good approximation of the system, and only simulations were used. Together, these yield a general picture of the conditions that promote coexistence in multiparasitoid-host systems. The effects of both lower and asymmetric within-host competition on coexistence have been neglected in existing theoretical models, and it is still an open question as to whether they promote or impair coexistence. In addition to elucidating the general effect of multiparasitism on host-parasitoid dynamics, our model may advance our understanding of why multiparasitism, though common in nature, so rarely leads to interspecific host sharing.

We then discuss the consequences of our results for the coexistence of *N. vitripennis* and *N. giraulti*. Specifically, we ask whether we can explain the persistence of *N. giraulti* in the face of competition with a superior competitor, with two of the three mechanisms described above. First, lowered within-host competition, while not giving an advantage to multiparasitism per se, may explain why *N. giraulti* is not outcompeted by *N. vitripennis* in the field. Second, an advantage in within-host competition may allow *N. giraulti* to compensate for its competitive disadvantage in other life-history traits; this would confer an advantage to multiparasitizing, as this competitive advantage is limited to multiparasitized hosts. This mechanism has been proposed to explain coexistence in several other systems (e.g., Amerasekare 2000; Cusumano et al. 2011; Mohamad et al. 2011), making a theoretical study of this scenario even more relevant. Thus, the former mechanism may explain only the persistence of *N. giraulti*, whereas the latter may additionally explain its preference for multiparasitizing.

Methods

We model a single host and two gregarious parasitoids with correlated distributions, assuming that offspring of both parasitoid species can emerge from a multiparasitized host. The basic model takes the following form:

$$\begin{aligned} H_{t+1} &= \lambda H_t \cdot f(V_t, G_t) \cdot e^{-dH_t}, \\ V_{t+1} &= c_V H_t (g_V + p_V g_{VG}), \\ G_{t+1} &= c_G H_t (g_G + p_G g_{VG}). \end{aligned} \tag{1}$$

Here, H_t, V_t, and G_t stand for the number of hosts and parasitoids at time t, where V and G can be interpreted as *Nasonia vitripennis* and *Nasonia giraulti*, respectively. The value λ is the intrinsic growth rate of hosts that escape parasitism, d is the density dependence of the hosts, and c_V and c_G give the fecundity of the parasitoids V and G. The values g_V, g_G, and g_{VG} denote the fractions of hosts parasitized by only V, only G, or both. The values p_V and p_G give the fraction of V and G in the offspring that emerge from multiparasitized hosts. Finally, $f(V_t, G_t)$ is the escape function, the fraction of hosts that escape parasitism by both species.

The escape function in a single parasitoid-host model is generally assumed to follow the negative binomial distribution. This assumes that hosts are found in patches; parasitoids are distributed among the patches, after which they search randomly within the patch (May 1978). This is a good approximation for *Nasonia* wasps, which parasitize the pupae of flies in animal carcasses and birds' nests and rarely find a second patch with hosts to parasitize (Grillenberger et al. 2008). In our model, we consider a system in which the distribution of the parasitoids over the patches is correlated, while encounters within the patch are random. This scenario can be approximated by a bivariate negative binomial distribution (Ives 1988*b*; Klopfer and Ives 1997), which has the following escape function:

$$f(V_t, G_t) = \left[\left(1 + \frac{a_V V_t}{k}\right)\left(1 + \frac{a_G G_t}{k}\right) - r\frac{a_V V_t a_G G_t}{k^2} \right]^{-k}. \tag{2}$$

The values a_V and a_G represent the two species' respective search efficiencies, and k is the clumping parameter determining the degree of spatial aggregation of the hosts and thereby the aggregation of encounters between hosts and parasitoids. If $k = \infty$, the negative binomial distribution reduces to a Poisson distribution (reflecting a lack of

spatial aggregation in the hosts), and lower values of k denote stronger aggregation. The host-parasitoid dynamics are stable when $k \leq 1$ (May 1978). Finally, r is the correlation between the distributions of the two parasitoids among the patches. A positive value for r denotes positive correlation in patch sharing between the two species, either because of interspecific attraction or because both species use the same cues to find a patch. Conversely, a negative value indicates interspecific avoidance.

Even if the distributions of the two species over the patches are strongly overlapping (high r), this does not necessarily mean that they share the same hosts within those patches. The covariance per host between the number of encounters of each species (number of hosts parasitized by each species), ρ, is given by

$$\rho = r\left(1 + \frac{k}{a_V V_t}\right)^{-1/2}\left(1 + \frac{k}{a_G G_t}\right)^{-1/2}, \tag{3}$$

which decreases with k (so stronger aggregation leads to a higher covariance) and increases with the mean number of encounters for both species ($a_V V_t$ and $a_G G_t$, respectively).

Calculating the fractions g_V, g_G, and g_{VG} is fairly straightforward. Because the total fraction of hosts encountered per species follows a negative binomial distribution, it follows that

$$\begin{aligned} g_V + g_{VG} &= 1 - \left(1 + \frac{a_V V_t}{k}\right)^{-k}, \\ g_G + g_{VG} &= 1 - \left(1 + \frac{a_G G_t}{k}\right)^{-k}. \end{aligned} \tag{4}$$

Because $g_V + g_G + g_{VG} + f(V_t, G_t) = 1$, the fraction g_{VG} can be derived from equations (2) and (4):

$$\begin{aligned} g_{VG} = 1 &- \left(1 + \frac{a_V V_t}{k}\right)^{-k} - \left(1 + \frac{a_G G_t}{k}\right)^{-k} \\ &+ \left[\left(1 + \frac{a_V V_t}{k}\right)\left(1 + \frac{a_G G_t}{k}\right) - r\frac{a_V V_t a_G G_t}{k^2}\right]^{-k}. \end{aligned} \tag{5}$$

From this and equation (4), the remaining fractions g_V and g_G can be derived:

$$\begin{aligned} g_V = &\left(1 + \frac{a_G G_t}{k}\right)^{-k} \\ &- \left[\left(1 + \frac{a_V V_t}{k}\right)\left(1 + \frac{a_G G_t}{k}\right) - r\frac{a_V V_t a_G G_t}{k^2}\right]^{-k}, \\ g_G = &\left(1 + \frac{a_V V_t}{k}\right)^{-k} \\ &- \left[\left(1 + \frac{a_V V_t}{k}\right)\left(1 + \frac{a_G G_t}{k}\right) - r\frac{a_V V_t a_G G_t}{k^2}\right]^{-k}. \end{aligned} \tag{6}$$

It also becomes clear from equations (5) and (6) that even if the distributions overlap perfectly ($r = 1$), this does not mean that all parasitized hosts are parasitized by both species; there always remains a fraction that is parasitized by V or G alone.

Between-Adult Competition

Adult female parasitoids compete over available hosts; we studied both symmetric and asymmetric competition where one species is competitively inferior, as appears to be the case for *N. giraulti*. Both scenarios were studied using a numerical analysis and individual-based simulations. A parasitoid's competitive ability is a combination of its search efficiency (a_V, a_G) and its fecundity (c_V, c_G); a difference in either can cause competitive asymmetry. In all simulations, we modeled competitive asymmetry by introducing a difference in fecundity between parasitoid species; their search efficiencies do not differ. We know from field data that *N. giraulti* has a lower fecundity than *N. vitripennis* (Grillenberger et al. 2009; Daoust et al. 2012), but nothing is known about their respective search efficiencies in the field, although *N. giraulti* appears to be less efficient in handling hosts in the lab (S. Pérez-Vila, personal observation). We expect to find the same results for asymmetry in fecundity and asymmetry in search efficiency; we tested this for part of the results and found only minor differences in the patterns found (results not shown).

Within-Host Competition

In the above model, c_V or c_G parasitoids emerge from hosts that have been parasitized by only one species. In the case of multiparasitism, the fractions of V and G emerging are given by p_V and p_G, which are functions of the average number of eggs laid per host by both species, E_V and E_G. These can be approximated by the total number of eggs laid per species (the total number of encounters multiplied by the number of eggs laid per encounter) divided by the number of hosts encountered by this species:

$$\begin{aligned} E_V &\approx \frac{a_V V_t c_V}{g_V + g_{VG}}, \\ E_G &\approx \frac{a_G G_t c_G}{g_G + g_{VG}}. \end{aligned} \tag{7}$$

Assuming the larvae of the two species are competitively equivalent, the fractions of emerging offspring from multiparasitized hosts, p_V and p_G, are then given by

$$\begin{aligned} p_V &= \frac{E_V}{E_V + E_G}, \\ p_G &= \frac{E_G}{E_V + E_G}. \end{aligned} \tag{8}$$

We analyzed the above system of equations numerically, determining whether there is a stable equilibrium where all three species coexist under either symmetric ($c_V = c_G$) or asymmetric ($c_V > c_G$) competition. The above equations make two critical assumptions. The first assumption is that the number of offspring emerging from parasitized hosts is always the same, regardless of how many parasitizations occurred. In *Nasonia* species, superparasitism is common (Molbo and Parker 1996; Grillenberger et al. 2008, 2009), and while females do avoid overcrowding and lay fewer eggs when superparasitizing (Wylie 1965; Werren 1980), more offspring emerge from superparasitized hosts than from single-parasitized ones (Molbo and Parker 1996). This suggests that hosts have a carrying capacity and that under natural conditions it can exceed the number of eggs laid by a single female.

The second assumption is that the larvae of *V* and *G* are competitively equal. While the relative competitive strengths of the two *Nasonia* species have not been studied, *N. giraulti*'s preference for multiparasitizing (S. Pérez-Vila, L. W. Beukeboom, R. S. Etienne, and B. W. Wertheim, unpublished manuscript) may reflect competitive superiority within the host. We used individual-based simulations to relax both assumptions and their effects on coexistence; the details are described in the simulation setup below.

Simulation Setup

We translated the above system into individual-based simulations for two purposes: to confirm the analytical results and to study scenarios that are not analytically tractable. We ran 50 replicate simulations for 20,000 generations, after which we recorded which parasitoids persisted for each individual simulation run.

Distribution of Encounters. For each host, the number of times it is encountered by each parasitoid species is drawn from a bivariate negative binomial distribution. This distribution is a compound of a bivariate gamma distribution with correlation coefficient r and a Poisson distribution; in biological terms, if $r > 0$, this means that the distribution of the parasitoids among patches is correlated, but the parasitoids search randomly within patches, as seems to be the case for *Nasonia* (Grillenberger et al. 2009). We used the method of Minhajuddin et al. (2004) for multivariate gamma sampling to generate bivariate gamma values x_1 and x_2 with correlation coefficient r, which are combined with independent Poisson distributions to draw the final number of encounters with each parasitoid species.

Parasitism and Within-Host Competition. For each encounter, the number of eggs laid by the parasitoid is drawn from a Poisson distribution with average c_V or c_G. After the parasitism phase, the survival rate of the eggs is determined by the total number of eggs ($E_{tot} = E_V + E_G$) and the host carrying capacity c_{max}. If $E_{tot} < c_{max}$, all larvae survive into adulthood. If $E_{tot} > c_{max}$ and both species have equal within-host competitiveness, the survival probability of each larva is $p_V = p_G = c_{max}/E_{tot}$.

Asymmetric within-host competition is implemented by giving *G* an advantage w_G when multiparasitizing, skewing the survival probabilities for offspring of the two species when they compete within the same host—in other words, the total number of emerging offspring remains the same, but the relative contribution of *G* is larger:

$$p_V = \frac{c_{max}}{E_V + w_G E_G},$$
$$p_G = \frac{c_{max}}{E_V/w_G + E_G}. \quad (9)$$

Larval survival in single-parasitized and superparasitized hosts is thus unaffected by the parameter w_G; competitive asymmetry occurs only within multiparasitized hosts. Little is known about the competitive interaction between *N. vitripennis* and *N. giraulti* within the host, and we make no specific assumptions about the underlying mechanism. Rather, any mechanism that causes either increased larval mortality for *V* (e.g., through larval aggression) or decreased larval mortality for *G* (e.g., through being a stronger competitor for resources within the host) may cause this type of competitive asymmetry.

In contrast with the numerical analysis of the equations, where the probabilities p_V and p_G are approximated by the average number of eggs per host, in the simulations these can be calculated exactly based on the actual number of parasitoids that parasitized each host. This can give a more accurate view on how within-host competition plays out and whether coexistence is possible.

Host and Parasitoid Reproduction. After parasitism, the number of hosts that escaped parasitism is subject to natural mortality (density dependence). The number that survives after this is multiplied by λ and rounded down, giving the size of the host population in the next generation. For all parasitized hosts, the number of eggs that develop to adulthood is summed to make up the two parasitoid population sizes in the next generation.

Results

Numerical Analysis

For the simplest case, symmetric competition where the two parasitoid species have the same fecundity ($c_V = c_G$), coexistence is possible no matter how strongly correlated the distributions are, as long as the host growth rate λ is

high enough to sustain the host and parasitoid populations (fig. 1*a*–1*d*). Next, we looked at the conditions for coexistence under asymmetric competition by introducing a fecundity difference (as seems to be the case for *Nasonia girault*i and *Nasonia vitripennis*). When the inferior competitor has a small fecundity disadvantage ($c_V = 5.1$, $c_G = 4.9$), the conditions for coexistence are far more restrictive, especially when the distributions are strongly correlated (fig. 1*e*–1*h*). Increasing the fecundity disadvantage for *G* ($c_V = 5.25$, $c_G = 4.75$) restricts coexistence even further (fig. 1*i*–1*l*). In general, coexistence is favored by a high host reproductive rate and strong host aggregation (low *k*).

Last, to get some impression of what would happen if within-host competition were lowered, we looked at the extreme and unrealistic scenario of removing within-host competition, by modifying the model so that all eggs laid by the parasitoids emerge as adults. In this case, because there is no competition between larvae within the host, the correlation

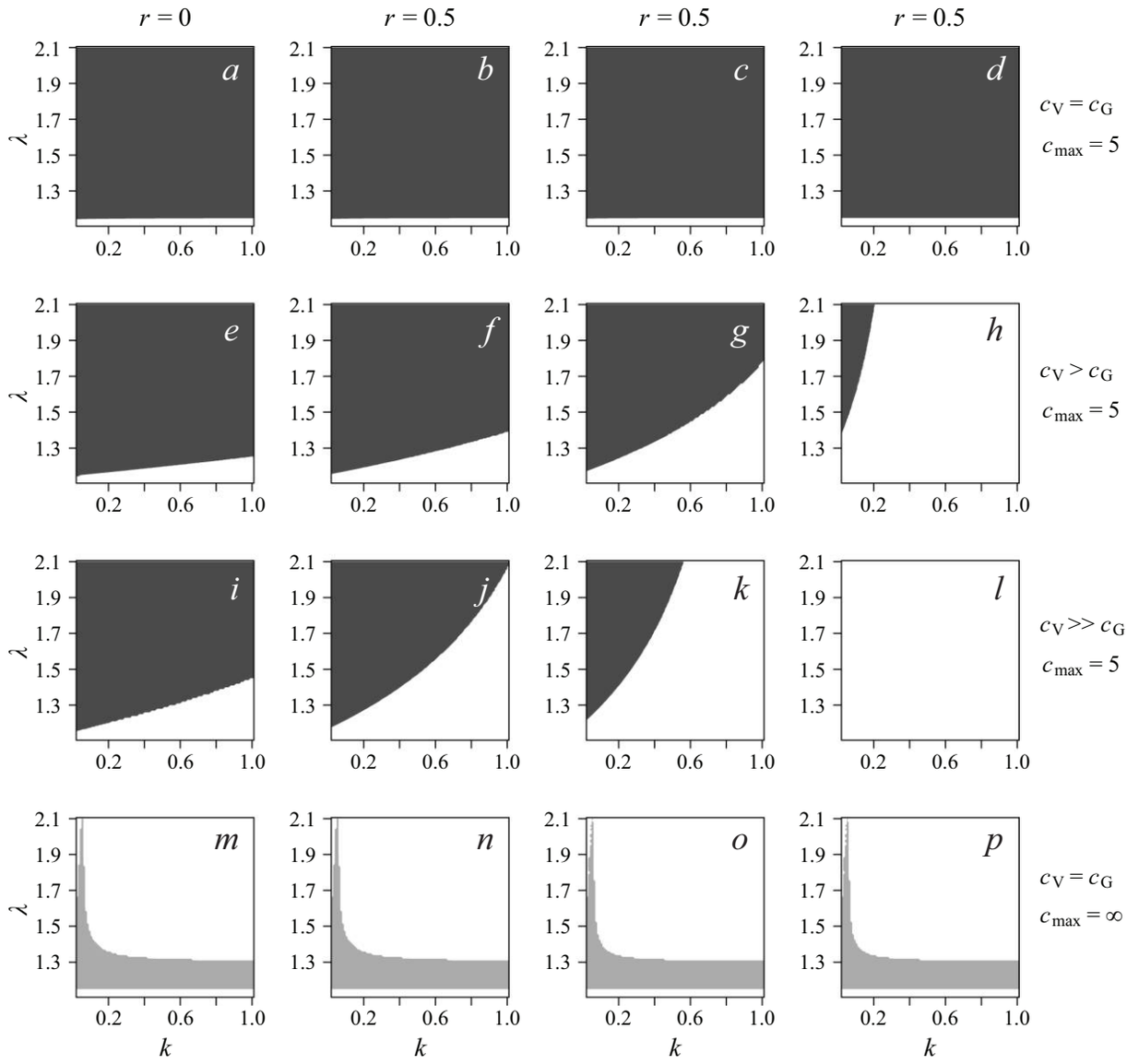

Figure 1: Numerical stability analysis of the one-host, two-parasitoid system for different values of the correlation coefficient *r* and the parasitoid fecundities c_V and c_G, plotted against the aggregation parameter *k* and host growth rate λ. White area = unstable; dark gray area = stable; light gray area = neutrally stable. In all panels, $a_V = a_G = 3 \cdot 10^{-5}$ and $d = 2 \cdot 10^{-5}$. *a–d*, $c_V = c_G = 5$. *e–h*, Small difference in fecundity, $c_V = 5.1$, $c_G = 4.9$. *i–l*, Large difference in fecundity, $c_V = 5.25$, $c_G = 4.75$. *a–l*, $c_{max} = 5$. *m–p*, No difference in fecundity and no within-host competition (all eggs laid emerge as adults), $c_V = c_G = 5$.

between the distributions (r) has no effect on the stability of coexistence. More importantly, the two-parasitoid equilibrium is never stable, although there is neutral stability for low host growth rate (fig. 1*m*–1*p*), but even then, long-term coexistence is not expected, because stochastic fluctuations in parasitoid abundances are expected to drive one of the parasitoid species extinct. Simulations confirm that there is never stable coexistence of the hosts and both parasitoids in this scenario. See the effect of increasing c_{max} in the next section.

Simulation Results

The simulation results generally confirm the results shown in figure 1 and discussed in the previous section (fig. 2*a*; $c_{max} = c_V = c_G = 5$). Although coexistence is not possible for all combinations of k and r, as figure 1*a*–1*d* shows, there is a still-wide parameter range for both parameters allowing coexistence of the two parasitoids. Coexistence is promoted by low k (strong aggregation of encounters) and low r (weakly overlapping distributions). When one species is competitively superior, coexistence is still possible but limited to a much narrower range for both k and r (fig. 2*b*), confirming the numerical results shown in figure 1*e*–1*l*.

Severity of Within-Host Competition

Now we go beyond the results of the numerical analysis, looking at the effect of varying the level of within-host competition by changing the within-host carrying capacity c_{max}. Decreasing within-host competition generally impairs coexistence; this effect is especially strong if one species (G) has a fecundity disadvantage (fig. 3*a*–3*d* for parasitoids with identical trait values and fig. 3*e*–3*h* for when G has a 10% fecundity disadvantage). In fact, low within-host competition (very high c_{max}) can destabilize the system entirely, making coexistence of the host with even one parasitoid species impossible (results not shown). Both of these destabilizing effects are most pronounced when host aggregation is weak (i.e., high values of k).

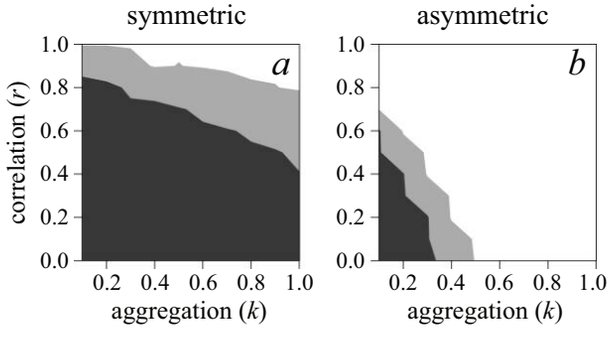

Figure 2: Simulation results showing whether the two parasitoids coexist after 20,000 generations for various values of aggregation k and correlation coefficient r. White area = never coexist; dark gray area = always coexist; light gray area = sometimes coexist (coexistence at the end of at least one simulation run). *a*, $c_{max} = c_V = c_G = 5$. *b*, $c_{max} = 5$, $c_V = 5.25$, $c_G = 4.75$. In both panels, $a_V = a_G = 3 \cdot 10^{-5}$, $d = 2 \cdot 10^{-5}$, and $\lambda = 1.3$.

Within-Host Advantage

Last, we studied the effect of a within-host competitive advantage (w_G) for G, which could compensate for its fecundity disadvantage. Again we chose the fecundities $c_V = 5.25$, $c_G = 4.75$ and studied values of w_G from 1.5 to 3.5 and two different values of the within-host carrying capacity c_{max} (6 and 10). We find that a within-host advantage can indeed facilitate coexistence (fig. 4), particularly for intermediate values of w_G. If the within-host advantage is too weak, it cannot compensate for the fecundity disadvantage; on the other hand, a very strong advantage makes it possible for G to outcompete V. This last effect is especially true when the distributions are strongly correlated (high r), because a higher correlation means that the two species will share the same hosts more often. This can be seen very clearly in figure 4*e*, where coexistence is possible only for an intermediate correlation. If it is too low, the two species will not interact enough to make the within-host advantage pay off, but if it is too high, G's advantage can drive V extinct.

Discussion

The results of our numerical analysis are in line with previous studies on the effect of aggregation and correlated distributions (Kakehashi et al. 1984; Klopfer and Ives 1997): coexistence is promoted by a high level of aggregation (low k) but reduced by overlap in the parasitoids' distributions (high r); this second effect is especially strong when there is competitive asymmetry between the species. All these results are in agreement with previous models that do not allow for interspecific host sharing (Ives 1988*b*; Klopfer and Ives 1997). The simulations generally show the same patterns as the numerical analysis, the main difference being that coexistence is consistently more restricted. Strongly overlapping distributions ($r \geq 0.8$) never support coexistence, and coexistence is even further limited when aggregation is relatively weak (for higher values of k). The difference between the numerical analysis and the simulations is that the survival probabilities p_V and p_G are approximated in equations (7) and (8) while the simulations keep track of the exact number of encounters. This introduces extra stochasticity in the simulations, reducing coexistence by increasing the probability of stochastic extinctions. Alternatively, if the approximations overestimate the contribution of the less common species, the numerical analysis may predict coexistence where this is not actually feasible. Because of its more exact formu-

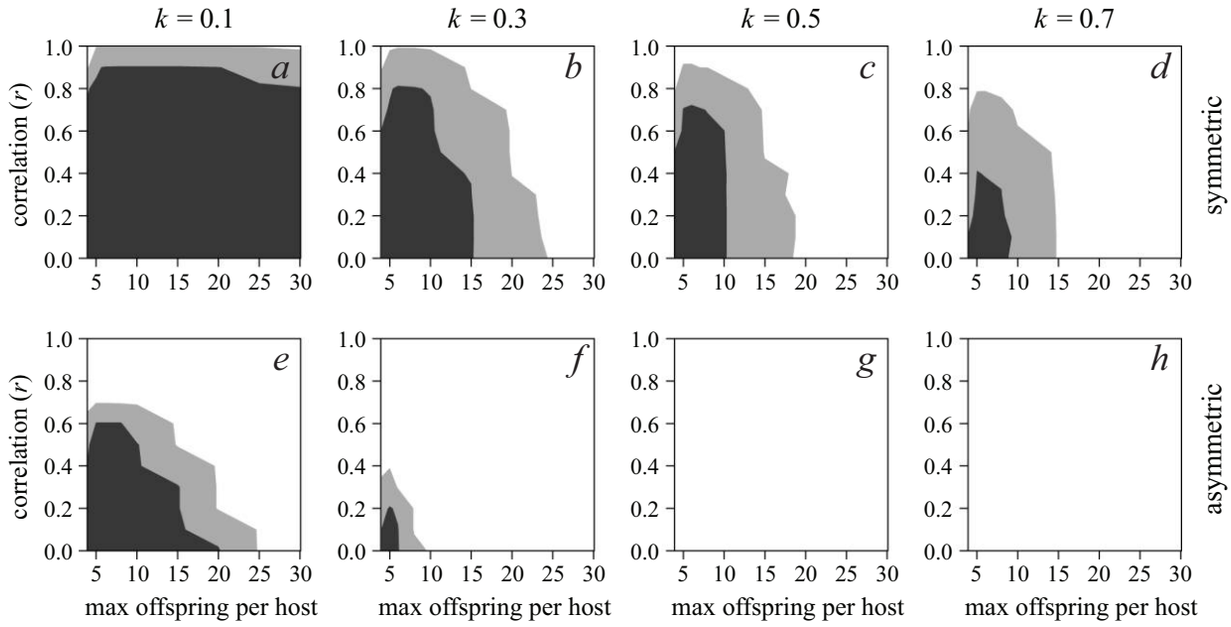

Figure 3: Simulation results showing coexistence of the two parasitoid species after 20,000 generations for various values of the maximum number of offspring per host c_{max} and correlation coefficient r. White area = never coexist; dark gray area = always coexist; light gray area = sometimes coexist (coexistence at the end of at least one simulation run). *a–d*, $c_V = c_G = 5$. *e–h*, $c_V = 5.25$, $c_G = 4.75$. *a*, *e*, $k = 0.1$. *b*, *f*, $k = 0.3$. *c*, *g*, $k = 0.5$. *d*, *h*, $k = 1$. In all panels, $a_V = a_G = 3 \cdot 10^{-5}$, $d = 2 \cdot 10^{-5}$, and $\lambda = 1.3$.

lation, the simulation results are likely a more accurate reflection of whether coexistence is possible.

In addition, we looked at two more factors that have previously received much less attention: severity and asymmetry of within-host competition. The former gives the counterintuitive result that stronger within-host competition promotes coexistence. This result was unexpected, as lower within-host competition may allow the two species to share the same host without a significant decrease in fitness. Thus, while increasing the within-host carrying capacity c_{max} lowers both inter- and intraspecific competition to the same degree, it may still be expected to have a positive effect on coexistence. We found the exact opposite result: removing within-host competition entirely—by setting within-host carrying capacity to infinity—made stable coexistence impossible, and coexistence was consistently promoted by stronger within-host competition. Resource limitation within the host proved to be critically important for coexistence: it always limits the more abundant species more strongly than it does the less abundant one, leading to a rare-species advantage that stabilizes coexistence. This also explains why coexistence is promoted by very strong aggregation (very low k), even though the degree of interspecific aggregation, as measured by the covariance ρ, increases for lower values of k (see eq. [3]): higher rates of superparasitism and multiparasitism increase the effect of within-host resource limitation.

Second, we found that in the case of competitive asymmetry (one species having a lower fecundity), an advantage in within-host competition could compensate for its competitive disadvantage and restore coexistence. However, the conditions that allow this are fairly restrictive. Most importantly, it is effective only when within-host competition is severe. Even if the within-host carrying capacity is only high enough that two parasitoids can share the same host without overcrowding ($c_{max} = 10$ in fig. 4), coexistence is restricted to a very narrow parameter range where the host distribution is very strongly aggregated.

General Implications for Coexistence

Our model yields several predictions for the effects of within-host competition on coexistence. Most importantly, it predicts that stable coexistence is possible only when within-host competition is severe. This is in direct contradiction to what we know of resource sharing in nature (i.e., that it is possible only when the offspring of a single female do not consume the entire host; Miller 1982; Magdaraog et al. 2012; Harvey et al. 2013); in terms of our model, this should mean that it is possible only when within-host competition is weak (high c_{max}). Strong within-host competition should lead to strong selection for mechanisms to eliminate heterospecific competitors, which is indeed commonly found in na-

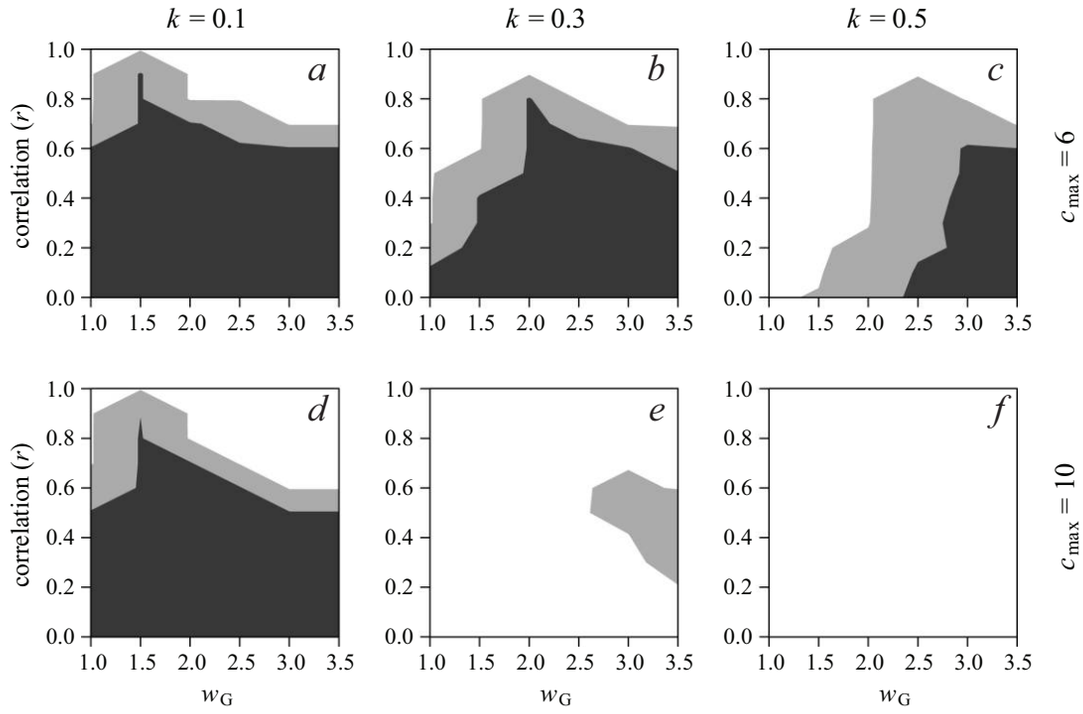

Figure 4: Simulation results showing coexistence of the two parasitoid species after 20,000 generations for various values of the competitive asymmetry w_G and the correlation coefficient r. White area = never coexist; dark gray area = always coexist; light gray area = sometimes coexist (coexistence at the end of at least one simulation run). In all panels, $c_V = 5.25$, $c_G = 4.75$, $a_V = a_G = 3 \cdot 10^{-5}$, $d = 2 \cdot 10^{-5}$, and $\lambda = 1.3$. *a–c*, $c_{max} = 6$. *d–f*, $c_{max} = 10$. *a*, *d*, $k = 0.1$. *b*, *e*, $k = 0.3$. *c*, *f*, $k = 0.5$.

ture, especially in solitary parasitoids (Godfray 1994). Therefore, our model gives a possible explanation for why interspecific host sharing is so rare in nature: the condition that enables it is the same condition that impairs stable coexistence.

Our model further predicts that interspecific resource sharing should be found when within-host competition is strong, but not so strong that such eliminating mechanisms have evolved. These conditions are mostly met by gregarious parasitoids, which indeed appears to be the case in nature (Sallam et al. 2002; Magdaraog et al. 2012). An exception was documented by Marktl et al. (2002), where resource sharing was found between a solitary and a gregarious parasitoid.

Similarly, the level of within-host competition is the most significant factor determining whether a within-host advantage can compensate for competitive inferiority on the adult level: this scenario is limited to severe within-host competition, the same condition that promotes the evolution of mechanisms for within-host superiority in the first place. The congruence of these conditions means that mechanisms to eliminate competitors should be common in nature, which is indeed the case (Godfray 1994). Moreover, the scenario where an inferior adult competitor can persist due to a within-host competitive advantage should be found mostly in solitary parasitoids. Indeed, nearly all recent studies demonstrating this scenario involve solitary parasitoids (Cusumano et al. 2011; Mohamad et al. 2011; Fernanda Cingolani et al. 2013; Mohommadpour et al. 2014), with a single exception where one of the parasitoid species is gregarious but has a very small brood size of one to three adults emerging per host (Amarasekare 2000). Thus, this prediction appears to hold up in nature as well.

Implications for Nasonia *Coexistence*

Our model was inspired by the coexistence of two *Nasonia* species competing for the same blowfly pupae in bird nests, with a very strong overlap in species distributions: *Nasonia girault* is found exclusively in association with *Nasonia vitripennis* (Grillenberger et al. 2009; Daoust et al. 2012). Given that *N. girault* is clearly the inferior competitor, having a lower clutch size in the field (Grillenberger et al. 2009; Daoust et al. 2012) and being slower in handling hosts (S. Pérez-Vila, personal observation), the fact that it can persist even though competition from *N. vitripennis* is very strong requires an explanation (Grillenberger et al. 2008).

There are several field data sets available to estimate the values of *k*. For *N. vitripennis*, the two reported values for

natural nests are similar ($k \approx 0.72$ [Grillenberger et al. 2008] for field data on only *N. vitripennis*; $k \approx 0.81$ [Grillenberger et al. 2009] for field data on *N. vitripennis* and *N. giraulti*). It is harder to estimate a value for *N. giraulti* because its abundance in the field is much lower, but Grillenberger et al. (2009) give an estimate of $k \approx 0.1$. If this is correct, this means that the encounters of *N. giraulti* are more aggregated than those of *N. vitripennis*. However, it should be noted that these estimates are based on data on emerged offspring, not on the actual distribution of encounters. There may be a discrepancy between these if not all parasitizations are successful, and this will particularly be the case if *N. giraulti* is facilitated by *N. vitripennis* and has a higher probability of successfully emerging when multiparasitizing. For this reason and because the field abundance of *N. giraulti* is much lower, its encounters may only appear to be more aggregated. Because the bivariate negative binomial distribution has only one value for k, it is difficult to estimate the correlation coefficient r with the available data. Using a weighted average of the two values, $k \approx 0.61$, we find an estimate of $r \approx 0.8$. This is consistent with the observation that *N. giraulti* is always found co-occurring in nests with *N. vitripennis* and never by itself, which indicates that r must be high to very high.

Our results show that the first of our hypothetical explanations for coexistence, weak within-host competition, does not hold up at all; to the contrary, weak within-host competition reduces the opportunities for coexistence. The second, a within-host advantage, has only a limited effect in promoting coexistence, mostly for intermediate distribution overlap. Given the strong overlap between *N. vitripennis* and *N. giraulti* in the field, this too seems unlikely to be the explanation for how *N. giraulti* can persist.

Limitations of the Model

Our model does not predict coexistence under parameter values for k and r that are realistic for the *Nasonia* system; evidently, our model may lack something else of vital importance to understanding coexistence of these two species. We make two critical assumptions: first, that encounters within patches are random, and second, that females always lay the same number of eggs, regardless of whether the host is fresh or already parasitized by either species. Regarding the first assumption, while field data on the distribution of foundresses over hosts showed no evidence of a preference for or against hosts used by other females (Grillenberger et al. 2009), laboratory experiments have shown that *N. vitripennis* avoids superparasitism when given the choice between fresh and parasitized hosts (Ivens et al. 2009; S. Pérez-Vila, L. W. Beukeboom, R. S. Etienne, and B. W. Wertheim, unpublished manuscript). The same is true for *Nasonia longicornis*, and a host choice experiment with *N. vitripennis* and *N. longicornis* showed that they both avoid multiparasitism even stronger than superparasitism (Ivens et al. 2009). The behavior of *N. giraulti* is very different: it appears to have no aversion to superparasitizing and a preference for multiparasitizing. Taking all of these data together, it appears unlikely that females use hosts within patches indiscriminately, as our model assumes. How nonrandom use of hosts—through either avoiding or preferring super- or multiparasitism—would affect coexistence is an open question. Avoidance of parasitized hosts would reduce within-host competition (although it would also reduce the number of available hosts, increasing adult competition), potentially lowering the negative effects of sharing a patch. On the other hand, it would lead to a more even distribution of encounters, reducing the level of aggregation (higher k) as well as reducing within-host competition. Both of these effects have been shown in this study to reduce coexistence rather than promote it. Whether either scenario would promote or reduce coexistence requires further study.

The second assumption, that females lay an equal number of eggs in parasitized and unparasitized hosts, is likely to be more critical. There is ample evidence that *N. vitripennis* adjusts its clutch size to lay fewer eggs when superparasitizing (Wylie 1967; Werren 1980, 1984; Ivens et al. 2009). Similar data are unfortunately unavailable for *N. giraulti*, but consistent with their apparent preference for multiparasitizing, they lay more eggs when multiparasitizing than *N. vitripennis* (S. Pérez-Vila, L. W. Beukeboom, R. S. Etienne, and B. W. Wertheim, unpublished manuscript). A version of the simulations in which both species lay fewer eggs in parasitized hosts, by either conspecifics or heterospecifics, did not yield any results suggesting that this alone would improve coexistence. Rather than reducing competition, this scenario leads to lost opportunities for superparasitizing females. The setup of our current model does not allow for females to look for a more suitable host after rejecting an unsuitable one or to offset the costs of laying fewer eggs in parasitized hosts by laying more eggs in unparasitized ones. A scenario that does allow for either of these two behaviors is definitely more realistic but is beyond the scope of our current study. A model explicitly allowing avoidance of or preference for parasitized hosts, through either oviposition or clutch size decisions, is a necessary direction for further study.

Last, it is possible that *N. giraulti*'s preference for multiparasitism reflects that it is facilitated by *N. vitripennis*, for example, if venom injected by *N. vitripennis* increases the survival probability of *N. giraulti* offspring. Such benefits to multiparasitism, where the offspring of the multiparasitizing female have higher survival due to injection of venom or polydnavirus, have been found in other systems (Guzo and Stoltz 1985; Cusson et al. 2002). It is unclear whether multiparasitizing confers any advantage of this kind to *N. giraulti*, but if this is the case, *N. giraulti* may benefit from

the presence of its competitor, potentially outweighing the costs. This may be especially relevant when combined with nonrandom host choice, as explained above.

Conclusions

This article aimed at studying the role of within-host competition on the coexistence of two parasitoid species sharing a host. We find three general patterns. First, coexistence is promoted by weak between-adult interspecific competition. Second, the opposite pattern was found for within-host competition: coexistence is promoted by strong within-host competition. Last, competitive asymmetry at the adult level reduces coexistence. If this is counteracted by asymmetry in within-host competition, with the species that is less competitive as an adult being a stronger competitor within the host, this can either promote or reduce coexistence, depending on the level of asymmetry and the amount of host use overlap.

Our model incorporating within-host competition was inspired by the *Nasonia* system. While the factors we studied seem unsuccessful in explaining coexistence in this particular system, they apply to multiparasitoid-host systems in general. The severity of within-host competition has been a neglected component of multiparasitoid-host models; this is the first model to look at its effects in detail, and we find that it can have a dramatic effect on whether coexistence of two parasitoid species is possible.

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